

STUDIES IN THE CORONULIDAE (CIRRIPEDIA):
SHELL MORPHOLOGY, GROWTH, AND FUNCTION, AND THEIR BEARING
ON SUBFAMILY CLASSIFICATION

RONALD MONROE
Queensland Museum*

ABSTRACT

A new morphological feature of the shell of *Chelonibia caretta* is described. A species *incertae sedis* is compared with *Cylindrolepas darwiniana* Pilsbry, 1916. *Cylindrolepas* may be a junior synonym of *Platylepas* on the basis of this comparison. The shell morphology and probable mode of growth of Coronulidae are described. A new arrangement of genera into subfamilies is proposed. The subfamily Coronulinae Leach, 1812, is emended to include *Coronula*, *Cetopirus*, *Cryptolepas*, and *Platylepas*. The subfamily Xenobalaninae Gruvel, 1903, is emended to include *Xenobalanus*, *Tubicinella*, *Stomatolepas*, and *Stephanolepas*. Chelonibiinae Pilsbry, 1916, and Emersoniinae Ross, 1967, remain unaltered, and Platylepadinae (auct.) is rejected. A possible phylogeny for the family is included.

INTRODUCTION

Monroe and Limpus (1979) indentified and listed the barnacle epifauna on turtles in Queensland Waters. Subsequent collection has yielded one other species of uncertain identity, and subsequent examination of specimens of *Chelonibia caretta* has clarified some aspects of shell morphology. Analysis of growth patterns and shell structure has thrown new light on the probable subfamilial relationships.

Specimen numbers prefixed by W refer to the Queensland Museum.

ADDITIONS TO SPECIES DESCRIPTIONS
OF MONROE AND LIMPUS, 1979.

CHELONIBIA CARETTA (SPENGLER, 1790)
(Plate 1, Figs. 1, 2)

MATERIAL EXAMINED

W3654, 15 specimens, North Reef, SE.Q.

Previous authors have remarked on the roughness of the exterior surface of the shell (e.g. Pilsbry 1916, Monroe and Limpus 1979). However, when the outer surface and base of cleaned specimens are examined, the roughness is attributable to infoldings of the outer wall (Plate 1, Fig 2, A). These structures are not present in *Chelonibia testudinaria* (Plate 1, Figs. 3, 4).

?*CYLINDROLEPAS DARWINIANA* PILSBRY, 1916
(Plate 1, Figs. 5–8; Plate 2, Figs. 1, 2)

From host number X9313, *Caretta caretta*, Mon Repos, 2.xi.1972, an empty shell was removed from the area round the base of the tail. In appearance the shell has obvious affinities with *Platylepas*. The midrib structure and the ridges of beading on the outer walls are very similar to those of *P. decorata*.

However the specimen also agrees well with Pilsbry's (1916) description of *Cylindrolepas darwiniana*, but not as well with his figures. These latter are not to the usual high standard of Pilsbry's drawings. It has not been possible to borrow the type of *Cylindrolepas darwiniana*, through no fault of the Academy of Natural Science Philadelphia. Pilsbry's (1916) description is reproduced below for comparison with the plates.

'The barnacle is hexagonal, the carinorostral diameter a little larger than the lateral, of about equal diameter from base to summit; whitish, with fine sculpture of close transverse wrinkles, and on the carina and carinolateral compartments a few low, coarse vertical ribs. The compartments

*Present address; 'Heather Cottage', Bradda Rd, Pt Erin, Isle of Man.

when isolated are square. Their summits are beveled and polished, apparently by wear. A median fold or filled sulcus is indicated on the polished summit by a small depression filled with the softer and dull substance of the outer layer; and on some compartments a slight, mesial sulcus is visible externally. The radii are represented by narrow sulci; their edges are distinctly septate. The lower edges of the compartments have about three short, vertical, blunt teeth on each side of a larger median tooth, which bends slightly inward, and is homologous with the prop or midrib in typical forms of *Platylepas*. The sheath is delicately striate transversely, and stops a little short of the basal edges of the compartments. The scuta are in contact with the terga, and together they stretch from end to end of the orifice. Carinorostal diameter, 4 mm; lateral diameter, 3.8 mm, height, 3 mm. Some individuals are slightly larger, greater diameter 5.3 mm.' . . .

'The specimens of *Cylindrolepas* were embedded in a very hard yellowish substance showing but little structure. Dr Thomas Barbour, of the Museum of Comparative Zoology, to whom I applied, concluded that it is the salt-water cured, sun-dried skin of either a loggerhead or green turtle, probably from between the neck and flippers or around the base of the tail.'

The main point of difference between Pilsbry's (1916) description and the photographs of the present specimen is the form and presence of the 'short, vertical, blunt teeth on either side of (the) larger median tooth.' One of these may be seen in Plate 1, Fig. 6, but the ratio of small to large is quite different to that shown in Pilsbry's figure. Nonetheless it is probable that the present material represents specimens of *Cylindrolepas darwiniana* — the first recorded since Pilsbry's description. If this is the case (as only comparison with the types will reveal) then, on shell characters, *Cylindrolepas* should be included in *Platylepas*.

SHELL MORPHOLOGY AND GROWTH WITH A DISCUSSION OF PROBABLE FUNCTION

Shells were cleaned in sodium hypochlorite solution. Histological specimens were decalcified in ethyl-diamine-tetra-acetic acid, stained with

Mallory's collagen stain, Hughesdon's modification (Carleton and Drury, 1957), and mounted in Canada balsam. The plates illustrating many of the morphological features discussed in this section are to be found in Monroe and Limpus (1979) to which much reference is made.

GENERAL REMARKS ON SHELL STRUCTURE

Barnacles of the family Coronulidae are diverse in shape and size. Some of them (subfamily Chelonibiinae) show relatively 'normal' balanomorph external morphology while at the other extreme is *Xenobalanus* with an external morphology reminiscent of the Lepadomorpha.

In common with other Balanomorpha the sheath in coronulids is laid down in zones of growth (Darwin 1854). The transverse striae so produced on the internal surface mark the lines of junction between successive periods of shell deposition — i.e. they mark moults. They are more distinct in some members of the family than others. Darwin (1854) clearly outlines the process of formation of the sheath.

In *Chelonibia testudinaria*, which has a thick outer wall and occupies a conventional balanomorph position on the surface of the host/substrate, the transverse striae are only apparent on the upper one third of the sheath (Fig. 1). In embedded species such as *Stomatolepas* sp. or *Stephanolepas muricata* with frail outer shells the transverse striae are apparent for the full depth of the sheath (Monroe and Limpus, 1979, pl. 2, 3, 6.). The striae may be closely placed as in *Platylepas decorata* (Monroe and Limpus, 1979,

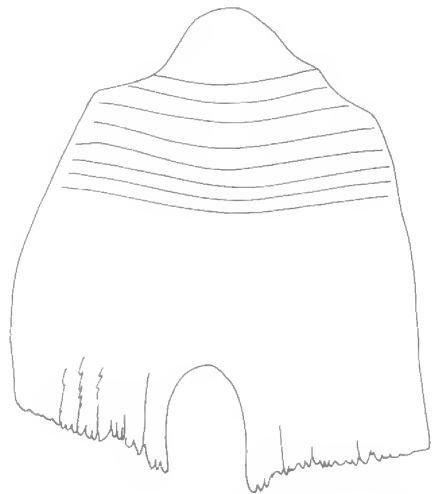


FIG. 1: A portion of the sheath of *Chelonibia testudinaria* showing transverse striae in upper portion.

pl. 4, fig. 8) or more widely as in *Stephanolepas muricata* (Monroe and Limpus, 1979, pl. 2, fig. 3).

It can be inferred from the appearance of transverse striae at different depths on the sheath that moulting in some superficially situated species (such as *C. testudinaria*) becomes less frequent with advancing age. However, in embedded species moulting continues at nearly constant frequency (as judged by the near regular spacing of the striae) throughout life. A corollary of this interpretation of striae spacing is that 'superficial' species remain on the host and continue to deposit shell for some time after their final moult whereas embedded species do not. This point is discussed later.

Pilsbry (1916) interpreted the morphology of coronulid shells as an adaptation to an impact prone situation. The massive shell of *Chelonibia* and the internal buttresses of *Platylepas* and the Coronulinae were seen as strengtheners of the shell. This view was shared by Ross and Newman (1967).

Darwin (1854) and Newman, Zullo, and Wainwright (1965) recognised that the complex wall folding of *Coronula* and *Cryptolepas* and the enclosed papillae of whale skin are a means of improving attachment of the barnacle to the whale. Darwin described and figured the ontogenetic development of this mechanism (Darwin, 1854, p. 15, figs. 4, 10). The latter authors also interpreted the six basal teeth of *Platylepas* as structures which 'lock the barnacle to the surface of the host to which it attaches' (Newman, Zullo, and Wainwright, 1965, p. 172).

Darwin (1854) recognised for *Tubicinella major* the role of the annular ridges as 'necessary to prevent too easy protrusion' of the shell.

It is here proposed that there are two mechanisms operating in the Coronulidae to facilitate attachment to the host — mechanisms adapted to the requirements of attaching to a growing substrate. Both mechanisms are derivations of the growth processes of the barnacle.

On the one hand there is the convoluted wall morphology of *Coronula* and *Cryptolepas*, and on the other hand there is the embedding process of *Tubicinella* spp., *Stomatolepas* spp., and *Stephanolepas muricata* with the concomitant requirement for regular moulting throughout life.

Platylepas spp. show elements of both processes, it being contended here that it is not the basal teeth but the whole shell wall which anchors the barnacle to its host.

One of the requirements for embedding in the

surface layer of an animal host is a means of overcoming the mechanical reaction of the host skin to the downward force of the growing barnacle. The holdfast structures of the established shell provide the necessary anchorage to permit downward growth as well as prevent dislodgement. How the fully embedded species initially gain a purchase to commence their burrowing is not clear from the adult shells available.

CHELONIBIA SPECIES

Chelonibia testudinaria and *C. caretta* are confined to hard areas of the skin of the host — carapace, plastron, and head. *C. testudinaria* attaches superficially and is not overlain by any host tissue. The large number of radial septae with their spiny lower margins (Pl. 1, Fig. 4) do not puncture the host scute but serve to increase the area of contact between the shell and substrate. That is, approximately two thirds (by inspection) of the base becomes effectively calcified and hence more firmly cemented to the substrate.

The forces most likely to dislodge a superficially attached barnacle are lateral — for example from water currents. The form and structure of the shell in *C. testudinaria* are well suited to reduce turbulence and improve adhesion.

When a large specimen of *C. testudinaria* is removed from the host it usually brings with it a portion of the keratinized layer of the scute showing that adhesion of the barnacle to the scute is greater than that of scute to host. However in the case of large (i.e. older) specimens of barnacles the host is probably nearer to moulting and the scutes could be expected to be loose at this time. Being a surface adherent *C. testudinaria* must be shed when host moulting occurs — approximately once a year (Limpus, in Lavery, 1978).

C. caretta has a shell structure and position on the host similar to those of *C. testudinaria*. However there are two differences notable in the context of this discussion: there is a layer of host keratin adherant to the outside of the shell wall which ascends to the level of erosion around the orifice (Monroe and Limpus, 1979, pl. 1, fig. 4), and the outer wall is roughened by longitudinal grooves and ridges (Pl. 1, Fig. 1).

These two features are allied. The longitudinal grooves when seen from their basal ends, appear as infoldings of the outer wall similar in structure to the median suture of *Platylepas* spp. (cf. Pl. 1, Figs. 1, 2 with Monroe and Limpus, 1979, pl. 3, fig. 8; pl. 4, fig. 1) (see below). Examination of the

host scute after removal of *C. caretta* shows that the keratinized layer has been split in two. The lower of these is the layer below the barnacle and is constantly being added to from below by the host epidermis. The upper layer is in keratin which invests the outer wall of the barnacle.

This upper layer is carried up the outer wall by being 'trapped' in the infoldings of the outer wall. *C. caretta* is more firmly attached to the host by virtue of this partial embedding. However since *C. caretta* does not penetrate the scute it will be shed at each host moult.

PLATYLEPAS SPECIES AND ?CYLINDROLEPAS DARWINIANA

Platylepas spp. maintain a more secure hold on the host than do *Chelonibia* spp. This is done by penetrating the scutes and soft epidermis of the host and anchoring the shell wall in the dermis and so resisting dislodgement.

The most prominent feature of *Platylepas hexastylus* is the median 'fold', 'sulcus', or 'midrib' or each compartment (Monroe and Limpus, 1979, pl. 4, fig. 3). During growth this structure traps the host scute at its outer end, and aided by the surface sculpture of the shell, carries the layer of scute up and outside the shell (Monroe and Limpus, 1979, pl. 3, fig. 7) in the manner of *Chelonibia caretta* (Monroe and Limpus, 1979, pl. 1, fig. 4). At the same time host scute is carried in between the walls of the fold and trapped. Along the lower edge of the fold, host fibrous connective tissue arising in the dermis is caught. There is no layer of scute below the barnacle. The same trapping of scute and dermis occurs at the compartmental sutures.

Along with the membranous basis the folds hold back the host tissues in a bowl-shaped cavity that allows the body of the barnacle to be partly below the host surface level and the shell to be of lower profile (Monroe, 1979, pl. 6, fig. 9 and pl. 2, fig. 3). The downward force to maintain the cavity may be exerted against the grip on the scutes.

Newman, Zullo, and Wainwright (1965, p. 172) have described the mode of growth of the buttresses of *Platylepas*. 'These are developed by allometric marginal growth increments. Lateral growth is suppressed at the location of each buttress so that it grows only downwards as the rest of the wall grows outwards and downwards'. That is the shell grows in diameter by the twelve lobes of the periphery pushing out into the host and trapping host tissue between themselves as they go. It is clear that the whole wall, and not just

the basal teeth, holds the barnacle so firmly to the host.

When the host moults its scutes, *P. hexastylus* is able to adhere because of its grip on the underlying dermal connective tissue.

Platylepas coriacea is very similar in shell structure to *P. hexastylus*. There is no host tissue on the outer surface of the shell as in *P. hexastylus* and all the anchorage appears to be provided by the nearly horizontal lower edges of the midrib folds. The leathery nature of the skin of the host — the leatherback turtle — may account for the failure of (or lack of necessity for) this species to embed.

P. decorata has midrib folds and props similar to those of the foregoing species but has more elaborate, and efficient, surface sculpture on the parietes to facilitate anchorage (Monroe and Limpus, 1979, pl. 4, fig. 7; pl. 6, fig. 8). Scute tissue becomes engaged in the rows of 'double beads' (cf. Monroe and Limpus, 1979, pl. 4, fig. 7, with pl. 2, fig. 4) and the median fold, while the props penetrate deeply allowing the barnacle to embed almost to its total depth.

?*Cylindrolepis darwiniana* is very like *Platylepas* and would appear, on the basis of the external shell morphology, to attach in a similar manner to *P. decorata*.

STEPHANOLEPAS MURICATA

In this species the simplest development of non-mural holdfast structures is found — blunt 'spines' (Monroe and Limpus, 1979, pl. 2, fig. 1, 2). Their position and structure are intimately associated with the pattern of growth of the shell wall. Once the barnacle has embedded the spines offer a secure mechanical grip on the host.

As outlined above, the outer wall and sheath are deposited in layers (Monroe and Limpus, 1979, pl. 2, fig. 3). In every second layer at both edges of each compartment an outgrowth is formed which curves upwards and reflects slightly back across the outer lamina of the compartment. On the radial side of the compartment these outgrowths are confluent with ridges that cross the radii and engage with the spines of the alar side of the contiguous compartment. These outgrowths become embedded in host connective tissue.

STOMATOLEPAS SPECIES

Stomatolepas spp. are similar to *Stephanolepas muricata*: the walls are thin and frail, and the barnacles are deeply embedded in the host. The outgrowths described in *Stephanolepas* are in *Stomatolepas* species much larger and completely

reflected back across the outer face of the compartments (Monroe and Limpus, 1979, pl. 2, fig. 8). There is also an outgrowth for each layer of the sheath. The projections are confluent with ridges on the radii (Monroe and Limpus, 1979, pl. 2, fig. 7). At the lower (growing) edge of the shell these reflected outgrowths are quite small (Monroe and Limpus, 1979, pl. 2, fig. 8), but successively higher (older) ones are longer with secondary outgrowths (scales) on their upper edges. By mid-height the reflected outgrowths from each side have met in the middle leaving a slight depression (Pl. 2, Fig. 5) which has been interpreted a residual rudimentary midline fold (Pilsbry, 1910).

The implications of this for the classification of the Coronulidae are discussed below. Pl. 2, Fig. 6 shows an histological section (radial) of a decalcified portion of the wall of *Stomatolepas praegustator*; Pl. 2, Fig. 7 is a similar tangential section. The space x represents the wall, the spaces y the reflected projections and the scales. Ct is host connective tissue and p the periostracum of the barnacle. The space enclosed between the reflected projections and the compartment wall is filled by host connective tissue. Connective tissue is also entwined around the scales, the whole mass forming a complex holdfast structure.

TUBICINELLA CHELONIAE

In this species the holdfast mechanism consists of large upward and outward curving blunt spines whose formation is described in Monroe and Limpus (1979) and Nilsson-Cantell (1932). This species, as does *Stephanolepas muricata* and *Stomatolepas* species, becomes completely embedded in the host.

THE WHALE BARNACLES

Darwin (1854) showed clearly the ontogeny of the holdfast arrangement of the walls of *Coronula diadema*, *C. regina*, and *Cetopirus complanata*. The process is similar to that in *Platylepas* and *Chelonibia caretta* in that it involves trapping of the upper epidermal layer in folds of the shell. It is probable that *Cryptolepas rhachianecti* can be included in this category also.

On the other hand *Tubicinella major* and *Xenobalanus globicipitis*, like *T. chelonie*, *Stomatolepas* spp. and *Stephanolepas muricata*, all 'burrow into' rather than 'grab hold of' the host epidermis. While acknowledging that *Cetopirus*, *Cryptolepas* and some *Platylepas* become covered

to a greater or lesser degree by host epidermis it is not the same process of burrowing as in *Tubicinella*, *Xenobalanus*, *Stomatolepas* and *Stephanolepas*.

HOST REACTION

Chelonibia species do not penetrate the host scutes and so there is no host tissue reaction. However *Tubicinella*, *Stomatolepas*, *Stephanolepas*, and to some extent *Platylepas*, all penetrate the basement membrane below the epidermis and invade the dermis. The host reaction is to lay down a capsule of fibrous connective tissue around the barnacle (Monroe and Limpus, 1978, pl. 2 fig. 1, and Pl. 2, Figs. 3-7). This is very thick and tough in the case of *Tubicinella cheloniae*. As the barnacle expands during growth the capsule becomes very tightly and intimately adherent to the barnacle shell. In the case of *Stomatolepas* spp., because of the action of the reflected projections and scales, the capsule is difficult to remove without damage to the shell and, while present, conceals the true nature of the shell structure (Pl. 2, Fig. 5). In *Platylepas hexastylus* and *P. decorata* the host capsule covers just the basal surface of the barnacle (Pl. 2, Figs. 3-4).

The host tissues are weakest at the interface of the dermal tissue and the capsule — the presumed site of growth of the capsule. It is at this interface that the host tissues yield when barnacles are removed from the host. This allows comparatively easy removal of the barnacle without damage to the host, except in the case of *Stephanolepas muricata*, and some *Platylepas* spp. which are deeply embedded on harder parts of the host. In these cases the host epidermis and scutes tend to grow back over the orifice of the barnacle enclosing it in a narrow-necked sack.

THE GROWTH STRATEGY OF EMBEDDED SPECIES

The remarks of this section are derived from a consideration of embedded species occurring on turtles but outline a growth strategy that probably applies also to embedded species on whales, e.g. *Tubicinella major* and *Xenobalanus globicipitis*.

The nature of the attachment region of the superficially situated *Chelonibia testudinaria* is not especially different from that of any other barnacle having a membranous basis and attaching on a hard surface. The same remark applies to the attachment of *Chelonibia patula* to the surfaces of its hosts — molluscs, xiphosurans,

and Crustacea (and old bones*). Though these barnacles are sloughed at moulting times and require a reproductive strategy to cope with this exigency, while on the host they are able to grow in the normal balanomorph fashion. *Chelonibia caretta* is more intimately attached to the upper stratum of its host, but there is still no necessity for special growth strategies.

The interface between these superficial barnacles and their hosts is, when compared to that of the species considered below, comparatively inert.

When embedded species are considered, i.e. those which penetrate into the dermal layer and are encapsulated by host connective tissue, it becomes apparent that the growth strategy of the normal balanomorph does not suffice. The barnacle would soon be 'grown off' the host by the connective tissue layer with which it is walled off by the host. The problem is analogous to a fish swimming upstream.

The barnacle, having established itself in the host, has to provide for its own increase in size, and also to grow a little faster than would otherwise be required in order to maintain its position against the sloughing process of the host.

Judging by scars on the host's surface it is possible for a barnacle to be completely sloughed

by the connective tissue capsule. In some cases barnacles may be sloughed because they have died and ceased to continue growing against the sloughing process. This is seen in the case of empty barnacle shells found in varying degrees of protrusion from the host.

The extra rate of growth required is expressed as shell height. Consider a barnacle B (Fig. 2a), with a host connective tissue capsule Ct, in host H. Assume that the barnacle is not at present growing but that the host capsule is active in sloughing the barnacle. After a time the barnacles will protrude a little above the host surface (Fig. 2b). Utilizing its purchase on the capsule and the adhesion of that to the host, the barnacle grows downward into the host, maintaining its position on the host, but the body is still at the upper end of the shell, attached by the opercular membrane, and this is projecting above the host surface (Fig. 2c). The barnacle now moults and the body is drawn down the shell, the upper portion of which

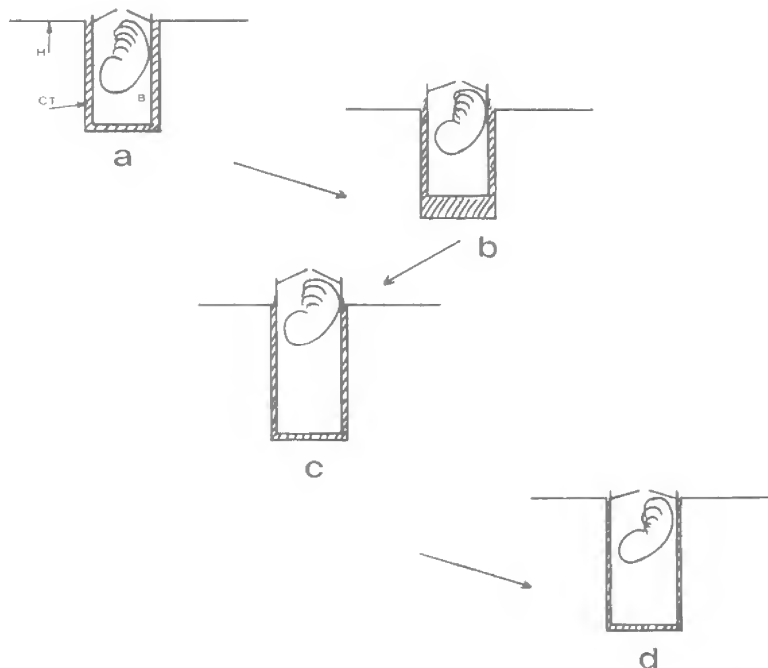


FIG. 2: Schematic drawing of mode of embedding of burrowing coronulidae in turtle hosts: H, host; CT, connective tissue capsule; B, barnacle. For explanation see text.

*Specimen lot W7354, *Chelonibia patula*, 20 individuals, was removed (together with 20 *Balanus trigonus* W7355) from a human femur recovered in 20 m from Moreton Bay near Moreton Is. on July 10th 1977. It may be that *Chelonibia patula* has a substrate preference involving organised calcium matrices.

flakes off along the weakness of the transverse striae in the sheath (Fig. 2d). The connective tissue capsule is degraded round the orifice, probably by the epidermal bacteria of the host. The wounds of *Tubicinella cheloniae* are specially septic.

It can be seen then that although there is a requirement in *Chelonibia* for the orifice to enlarge by erosion in the early period of the barnacle's adult life, facilitated by the weaknesses of the transverse striae and growth of the radii, at maturity this is no longer so. However in the embedded species, continued moulting and growth are required — radial growth maintaining shell diameter, and moulting, with loss of the protruding shell, maintaining the barnacle's position on the host.

DISCUSSION

SUBFAMILY CLASSIFICATION

Definitions and component taxa of three of the four previously accepted subfamilies within the Coronulidae have been given by Newman and Ross (1976) and were used by Monroe and Limpus, 1979. A definition of Platylepadinae was omitted by Newman and Ross, 1976. Zullo (1963) had previously proposed such a subfamily using Pilsbry's (1916) definition of the platylepad series. Newman and Ross's (1976) list of genera within their Platylepadinae is the same as that for Pilsbry's platylepad series and presumably their subfamily would rest upon the same definition.

Further discussion of the authorship of the Platylepadinae will not be undertaken here as morphological information from this study casts doubt upon its integrity as a grouping. The previously accepted subfamilies and their characters are presented in Table 1.

The prime character separating the Platylepadinae from the other subfamilies is the presence or absence of a median sulcus, midrib, or a vestige thereof (Pilsbry, 1916; Zullo, 1963). The

presence of this character has been claimed in *Platylepas*, *Cylindrolepas*, *Stomatolepas*, and *Stephanolepas*. It is certainly present in *Platylepas* (Monroe and Limpus, 1979, pl. 3, fig. 8, pl. 4) are most likely in *Cylindrolepas* (see *Cylindrolepis darwiniana* and Pl. 1, Figs. 5–6). However it is clearly absent from *Stomatolepas* and *Stephanolepas* (Monroe and Limpus, 1979, pl. 2; pl. 3, figs. 1–5). No vestige or precursor of such a structure can be detected. Pilsbry's (1910; 1916) interpretation of the mid compartmental groove in *Stomatolepas* as a rudimentary sulcus is due in his misunderstanding of the mode of growth of the external sculpture. Also he observed shells clothed in connective tissue (as judged by his paratypes) which hinders observation (cf. Pl. 2, Fig. 5 with Monroe and Limpus, 1979, pl. 2, fig. 4). Pilsbry (1916) never saw *Stephanolepas* but inferred from Fischer's (1886) description of smooth mid compartmental areas that it would be similar to *Stomatolepas*.

Similarly a median fold or sulcus is said to be absent in the other subfamilies. However structures very similar in formation and function to the median fold of *Platylepas* can be detected in *Chelonibia caretta* (Pl. 1, Fig. 2).

The Coronulinae are united by the presence of an 'oral hood' (Darwin, 1854, pl. 17, fig. 4a) and the possession of a 'single row of wall tubes formed by infoldings of (the) outer lamina against the sheath' (Newman and Ross, 1976, p. 37).

Much confusion has been brought about by the terms 'infolding' and 'outfolding'. Setting aside the Chelonibiinae and Emersoniinae, which have more recently been included in the Coronulidae, the main division in the Coronulidae, between the Platylepadinae and Coronulinae, has been based chiefly on the type of wall folding. The following paragraphs show that 'in' and 'out' are relative terms that have obscured the similarity between some genera of the Coronulidae.

In *Tubicinella*, tubes (interlaminar pores) are formed by the union of lateral outgrowths from

TABLE 1: THE SUBFAMILIES OF THE CORONULIDAE AND THEIR DISTINGUISHING CHARACTERS (AFTER NEWMAN AND ROSS, 1976, AND ZULLO, 1963).

Subfamily	6 or 8 wall plates	opercular plates weakly articulated	oral hood +/-	tergum reduced	rows of wall tubes	mid-parietal sulcus
Chelonibiinae	6/8	yes	-	+	1	-
Emersoniinae	6	?	?	?	several	-
Platylepadinae	6	yes	-	+	not specified	+
Coronulinae	6	yes	+	+++	1 (wall folds)	-

the outer edges of the interlamine septa (Darwin 1854). There are no 'infoldings' of the wall in the sense of Newman and Ross (1976). *Xenobalanus* has incomplete interlamine pores (Pl. 2, Fig. 8) but no 'infoldings' of the outer layer. In *Coronula* and *Cetopirus* such interlamine pores exist (Darwin 1854) as well as a 'single row of tubes formed by infoldings of the outer lamina against the sheaths' (Newman and Ross, 1976, p. 37). In *Cryptolepas* (which has interlamine pores (Pilsbry, 1916)) these 'infoldings' produce an incomplete outer wall analogous with that of *Coronula* (Pilsbry, 1916, p. 280, pl. 66).

As shown above *Stomatolepas*, *Stephanolepas*, *Tubicinella* and *Xenobalanus* have no wall folding. What is more, they are all united by other characters: 1, possession of structures arising from the lateral edges of the compartments and forming holdfasts (this is not strictly so in *Tubicinella major* as the annular ridges are formed across the whole of the face of the compartment. The ridges are, however, produced in synchrony with the layers of sheath as are the holdfasts on the other genera included here); 2, the shell is completely embedded in the host, is thin-walled and frail, and grows continually and rapidly (as judged by the relatively wide layers of the sheath) to maintain its position on the host; and 3, the shell is conical; straight sided and only slightly tapering in *Tubicinella*, 'glubulo-conic' (Fischer, 1886) and more strongly tapering in *Stomatolepas* and *Stephanolepas*. Since only three or four sheath layers of *Xenobalanus* are retained at any one time (Pl. 2, Fig. 8) it is difficult to determine if or how the shell tapers, but in general shape it is in conformity with those of the other genera.

Platylepas is said to have an 'infolded' buttress (Pilsbry 1916; Newman, Zullo, and Wainwright, 1965) and this is a convenient way to describe the buttress — especially that of *P. hexastylus* when seen from the exterior, e.g. Monroe and Limpus, 1978, pl. 4, fig. 3. However when seen in basal view, Monroe and Limpus, 1979, pl. 4, fig. 1 the inner edge of the buttress (except in the carina) aligns well with the plane of the intercompartmental sutures (roughly a cylinder), and the lower projection of the buttress — curving in under the lower edge of the sheath — is strongly reminiscent of the structure of *Cetopirus complanata* of which (as *Coronula balaenaris*) Darwin (1854, p. 416) says 'the inner ends of the folded walls . . . descend some little way beneath the basal edge of the sheath, as low, or lower, than the circumference of the shell' (Darwin, 1854, pl. 16, fig. 3). *Platylepas* could be interpreted as a *Coronula* with two

outfoldings in each compartment. Whereas in *Coronula* the space between the two layers of the outfolded outer lamina is narrow and filled by calcareous material, in *Platylepas*, they are wide, though still solidly filled. The 'tubes' in *Coronula*, filled with whale epidermis, are homologous with the narrow space between the walls of the buttress in *Platylepas* in which turtle host tissue is held.

Newman, Zullo and Wainwright (1965, p. 172) recognise that 'in *Platylepas* the regions occupied by the buttresses . . . correspond to the "canals" in the whale barnacles' and that, 'in *Coronula* and *Cryptolepas*, the intervening growth areas (between the canals) . . . could be called buttresses, but they are homologous with the wall proper, rather than the buttresses of *Platylepas*', but they fail to realise the implication of this homology for the classification of the Coronulidae. There has been so much attention focused on the 'infoling' of buttresses in *Platylepas* and the 'outfolding' to form 'canals' in *Coronula* and *Cryptolepas* that, coupled with a lack of understanding of the function of these structures in *Platylepas*, it has led to the obscuring of the close relationship between these genera. The walls of *Platylepas*, *Coronula*, *Cetopirus*, and *Cryptolepas* are homologous in both structure and function.

On the basis of wall structure then, a second group of genera can be recognised composed of *Coronula*, *Cetopirus*, *Cryptolepas*, *Platylepas* and *Cylindrolepas*.

The remaining genera, *Chelonibia* and *Emersonius*, are at present accommodated in their own subfamilies. *Emersonius cybosyrinx* is a fossil form and is not considered further here. The inclusion of the Chelonibiinae in the Coronulidae is not questioned, and is supported by the presence of involutions in the outer lamina of *Chelonibia caretta* which this study has revealed (Pl. 1, Fig. 1).

The arrangement of subfamilies in the Coronulidae proposed as a result of this study follows.

CORONULINAE LEACH 1812, EMEND.

Wall of 6 plates, exterior lamina of wall folded to produce holdfast structures by trapping host epidermal tissues, attached to surface of host or only shallowly embedded. *Coronula*, *Cetopirus*, *Cryptolepas*, *Platylepas*, *Cylindrolepas*.

XENOBALANINAE GRUVEL, 1903, EMEND.

Walls of 6 plates, holdfast structures produced by outgrowths from edges of compartments in

hosts but now include species which occur on hosts from turtles to whales (fig. 3).

Chelonibia.

Emersonius.

Ross and Newman (1967) proposed a phylogeny for the Coronulidae in which the more generalised 'primitive' chelonibiines exploited the phylogenetically older hosts (Crustacea and molluscs) while the more advanced coronulines were confined to more recent hosts — cetaceans.

The scheme suggests coevolution of the Coronulidae and the major groups of marine vertebrates, the 'higher' subfamilies of barnacles supposedly arising as new host forms became available.

In the light of the above proposed altered subfamily classification it is appropriate to re-examine the probable phylogeny of this family.

Under the proposed classification the Coronulinae are no longer epizooans only of cetaceans but are to be found on phylogenetically 'older' hosts such as turtles. Similarly the Xenobalaninae (which in part takes the place of the Platylepadinae) are no longer confined to the 'middle' range of

Ross and Newman (1967, p. 16) maintain that 'the most generalised members of (the Coronulidae) are *Platylepas* and *Chelonibia patula*'. If epizootes are host conservative then *Chelonibia patula* would be a candidate for the position of most generalised coronulid. *Platylepas* however shows all the attributes of the (generally accepted) more advanced *Coronula* (see above).

It is possible to see a relationship between the Chelonibiinae and Coronulinae in the involutions of the exterior wall of *Chelonibia caretta* and the convoluted exterior wall of the coronulines. It is also possible to see a relationship between the Chelonibiinae and Emersoniinae in the well developed radial septae of both groups. However it is not possible to recognise any general morphological affinity of the Xenobalaninae with the above three subfamilies except in the possession of porose walls by some of the xenobalanines and an epizooic habitat.

Figure 4 shows an inferred phylogeny of the Coronulidae based on wall structure and function. The ancestral form is postulated as being similar to *Chelonibia patula*, having porose walls, and radial septae projecting into the cavity of shell. *C. testudinaria* is similar in construction to *C. patula* but has further developed radial septae and the pores in the walls are filled with calcareous matter in the upper parts.

The Emersoniinae are separated from the chelonibiid stock by the formation of intercalary and transverse septae. The Coronulinae arise from the chelonibiid stock somewhat later, there being a strong similarity in the structure and function of the involutions in the outer wall of *C. caretta* and the convoluted wall of the Coronulines. *C. manati* is supposed, on the basis of Pilsbry's 1916 description, to have similar involutions.

Whence the Xenobalaninae arise it is difficult to say. Since they are all burrowing forms they are unlikely to be associated with the 'older' exoskeletal hosts. It is possible that they do not belong in the Coronulidae, but considerations of the anatomy of the soft parts make that improbable.

Darwin (1854) makes note of the 'beaded' nature of the sculpture on the exterior of *Coronula* and *Platylepas*. These beads are synchronous with the layers of the sheath and can be quite elaborate — e.g. in *Cryptolepas rachianecti* (Pilsbry, 1916, pl. 66) and? *Cylindrolepas darwiniana* (Pl. 1, Figs. 5, 6). It may be that the Xenobalaninae arose from a stock in which the radial septae were

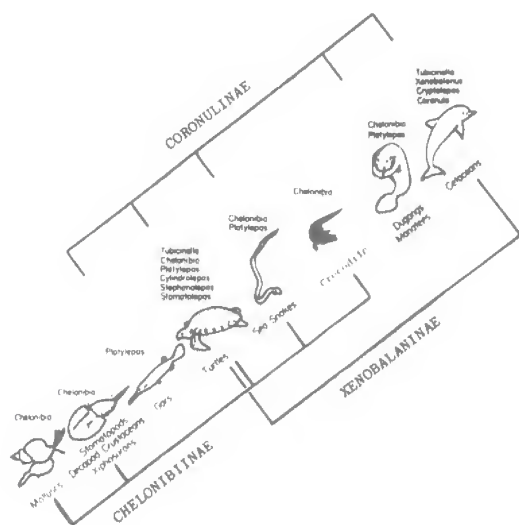


FIG. 3: The relationship between hosts and subfamilies proposed as a result of this study.

suppressed and there was no development of wall convolutions, the development of the holdfast structures taking place by the elaboration of the 'bead' structure at the edges of each compartment. In *Tubicinella major* the annular ridges may be an expression of the growth ridges as seen across the exterior of the compartments in other species — e.g. *Platylepas hexastylus* and ?*Cylindrolepas darwiniana*.

The presence of an oral hood in *Tubicinella major* and *Xenobalanus* in the Xenobalaninae on the one hand and in *Coronula*, *Cetopirus* and *Cryptolepas* in the Coronulinae on the other is an objection to the proposed arrangement of the genera. This structure though, may be developed only in those species occurring on whales as an adaptation to the higher swimming speeds of these hosts.

CONCLUDING REMARKS

The Coronulidae are a very specialized group of barnacles. In the main, they exhibit a high degree of host and site specificity. The principal hosts, turtles and whales, are migratory animals, in some

cases traversing many degrees of latitude in their migrations. The coronulids occurring on these animals can hardly be considered as sessile animals in the sense of the 'normal' barnacle. While it is true that *Lepas* species are to be found only on floating substrates, it can at least for them be pointed out that the substrate moves with nearly the same vagaries as the general body of water around them. Only *Conchoderma virgatum* (Spengler, 1790), an epizooite of epizooites, and *Analesma squalicola* (Love, 1844), share with the coronulids 'active' motion through the water as being normal for the entire population. This fact prompts questions about the breeding biology of the Coronulidae. When are larvae released? Perhaps in synchrony with host aggregations. How long is their pelagic life? The only published information available is for *Chelonibia patula* (Crisp and Costlow, 1963) and that species is found attached to relatively localised hosts — crabs and molluscs.

It was observed during the summer at Mon Repos that newly settled and small *Chelonibia testudinaria* were comparatively abundant (C.

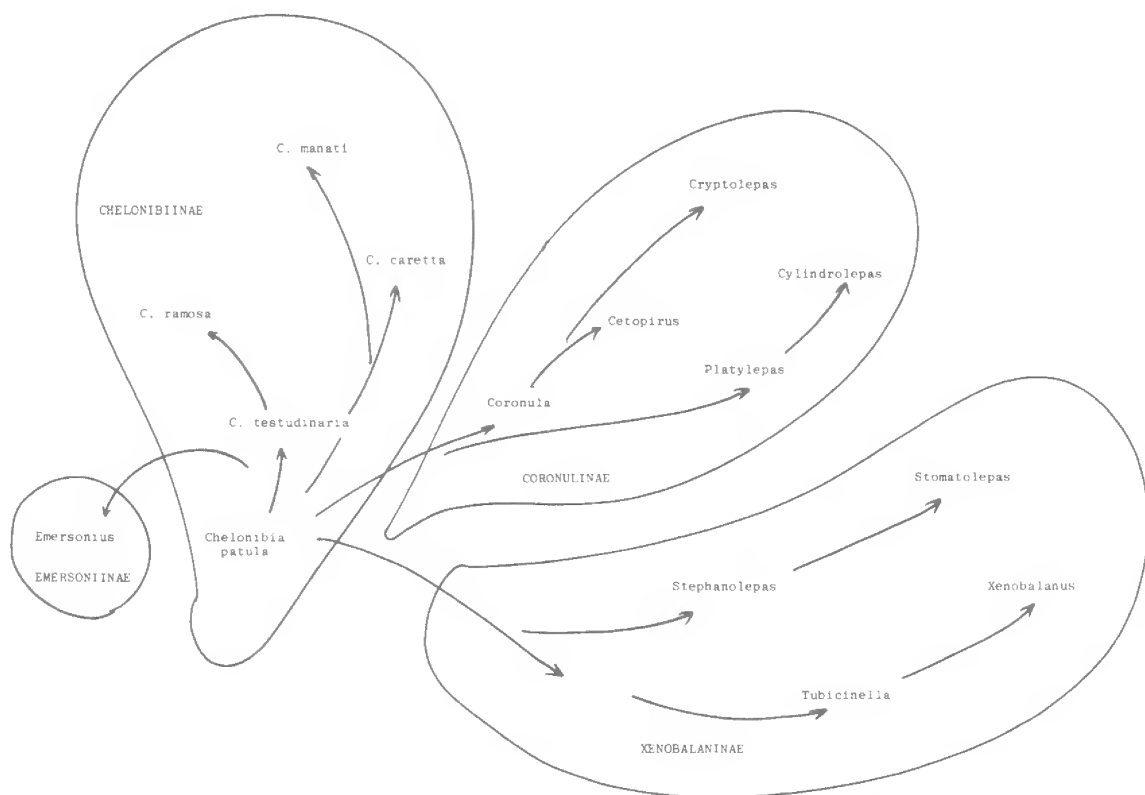


FIG. 4: A possible phylogeny of the barnacles of the family Coronulidae.

Limpus, pers. comm.) which lends some support to the idea that larvae are released during aggregation of the hosts on the breeding grounds.

Some species of coronulid are comparatively rare — e.g. *Stephanolepas muricata* and *Tubicinella cheloniae*. What mechanisms operate to ensure sufficient settlement of larvae is not known. These two species are embedded in firm tissues underlying hard epidermal structures. *T. cheloniae* penetrates the dermal bone of the carapace. Tomlin (1967, not seen, reported in Mitchell and Kozicki, 1975) cites L. Mathews to the effect that an enzyme is secreted by *Tubicinella major* which dissolves skin proteins 'which they then probably consume'. If such a mechanism operates in *T. major* to facilitate embedding (though there is no evidence of reduced feeding ability, as judged by the cirri) a similar one may be present in other Xenobalaninae.

Barnacle cyprids respond positively to specific proteins, arthropodins, but these active substances are not confined to arthropods alone (Crisp 1974). What substance(s) provides the stimulus to settlement of coronulids is not known. The mechanism of site selection on the host is not known though it is possible that turbulence may play some part in defining areas on the host suitable for particular species of barnacles.

ACKNOWLEDGMENTS

Thanks are due to the following Queensland Museum staff who provided assistance with this study: Mr. N. Hall who cut the histological sections; Messrs. A. J. Easton and R. Burgess who printed the photographs; and Mr. B. M. Campbell and Dr. L. J. Cannon for valuable advice, criticism, and encouragement. Dr. J. G. Greenwood, Zoology Department, University of Queensland, is especially thanked for advice and help in the course of this study.

LITERATURE CITED

- CARLETON, H.M. AND DRURY, R.A.B., 1975. 'Histological Technique'. Oxford University Press: London. 343 p.
- CRISP, D.J., 1974. 'Factors influencing the settlement of invertebrate larvae', p. 177–265 in GRANT, P.T., and MACKIE, A.M., (Eds) 'Chemoreception in Marine Organisms'. Academic Press: London. 295 p.
- DARWIN, C., 1854. 'A Monograph of the subclass Cirripedia with figures of all the species, the Balanidae'. The Ray Society: London. viii + 684 p.
- FISCHER, P., 1886. Description d'un nouveau genre de Cirrhipedes (*Stephanolepas*) Parasite des tortues marines. *Actes Société Linnéenne Bordeaux*. (4)10: 193–6.
- MITCHELL, E. AND KOZICKI, V.M., 1975. Autumn strandings of the northern bottlenose whale (*Hyperoodon ampullatus*) in the Bay of Fundy, Nova Scotia. *J. Fish. Res. Board Can.* 32(7): 1019–1040.
- MONROE, R.W., 1979. Studies in the Coronulidae: Barnacles on Turtles in Queensland Waters. Unpubl. M.Sc. Thesis, Zool. Dept. Univ. Qd.
- MONROE, R.W. AND LIMPUS, C.J., 1979. Barnacles on turtles in Queensland waters, *Mem. Qd Mus.* 19(3): 197–223, pls. 1–6.
- NEWMAN, W.A. AND ROSS, A., 1976. A Revision of the balanomorph barnacles; including a catalogue of the species. *Mem. San Diego Soc. Nat Hist.* 9: 1–108.
- NEWMAN, W.A., ZULLO, V.A., AND WAINWRIGHT, S.A., 1965. A critique on recent concepts of growth in the Balanomorphs (Cirripedia, Thoracica). *Crustaceana* 12: 167–178.
- NILSSON-CANTELL, C.A., 1932. The Barnacles *Stephanolepas* and *Chelonibia* from the turtle *Eretmochelys imbricata*. *Ceylon Journal Science*, Sect. B. (*Spolia Zeylan*). 16(3): 257–64, 3 pls, 2 figs.
- PILSBRY, H.A., 1910. *Stomatolepas*, a barnacle commensal in the throat of the Loggerhead turtle. *Am. Nat.* 44: 304–6.
1916. The sessile barnacles (Cirripedia) contained in the collections of the U.S. National Museum, including a monograph of the American species. *Bull. U.S. Nat. Mus.* 93: 1–366, pls. 1–76.
- ROSS, A. AND NEWMAN, W.A., 1967. Eocene Balanidae of Florida, including a new genus and species, with a unique plan of 'turtle-barnacle' organisation. *Am. Mus. Nov.* 2288: 1–21.
- ZULLO, V.A., 1963. Classification and Phylogeny of the Balanomorphs (Cirripedia). Ph.D. thesis, University of California, 372 p. University Microfilms: (Ann Arbor and London).

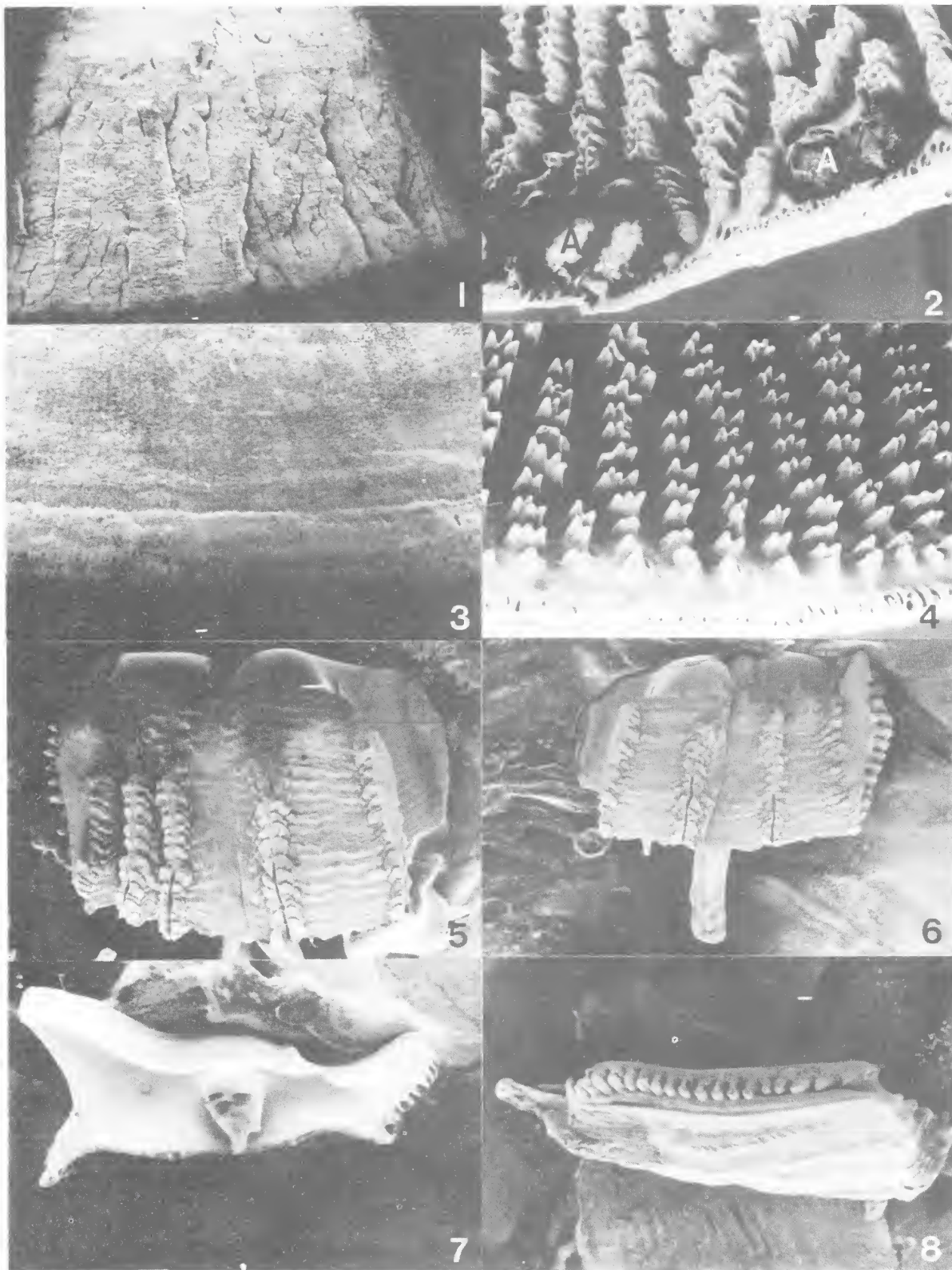
MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE I

FIGS. 1-2: *Chelonibia caretta* (Spengler), W3654; 1, basal edge of exterior of shell showing grooves; 2, peripheral edge of base showing infoldings of outer layer (A).

FIGS. 3-4: *Chelonibia testudinaria* (Linnaeus), W7845; 3, basal edge of exterior of shell; 4, peripheral edge of base.

FIGS. 5-8: ?*Cylindrolepas darwiniana*, W7848; 5-6, exterior of compartments; 7, basal view; 8, radial edge of compartment.



MEMOIRS OF THE QUEENSLAND MUSEUM

PLATE 2

- FIGS. 1–2: ?*Cylindrolepas darwiniana* W7848; 1, opercular view of compartment; 2, radial edge of compartment.
- FIG. 3: *Platylepas hexastylus* (Fabricius), W7814; section of decalcified animal showing a, cavity of shell, ct, connective tissue capsule of host, k, keratin layer of host epidermis, p, periostracum of shell.
- FIG. 4: *Platylepas decorata* Darwin, W7811; approximately median radial section of one wall illustrating intimate association of keratin of host, k, with the fine 'beaded' sculpturing on the exterior of the parietes, s, the basal membrane, b, is covered by host connective tissue, ct.
- FIG. 5: *Stomatolepas praegustator* Pilsbry, exterior view of compartment with investing layer of host connective tissue.
- FIG. 6: *Stomatolepas praegustator* Pilsbry, W7815; radial section of decalcified wall, x, reflected projection, y, host connective tissue, ct, and barnacle periostracum, m.
- FIG. 7: *Stomatolepas praegustator* Pilsbry, W7813; tangential section of decalcified wall, symbols as in fig. 6.
- FIG. 8: *Xenobalanus globicipitis* Steenstrup, W7384; exterior view of a compartment showing incomplete fusion of outer lamina.

